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THE ATLANTIC COASTAL PLAIN ELEMENT IN THE FLORA OF THE GREAT LAKES.

Donald Culross Peattie.

It has long been known that the flora of the sand dunes and shores of the Great Lakes, and particularly of those at the head of Lake Michigan, contains some remarkable elements, for the vegetation of this area is often in sharp contrast to that of the bordering forest and prairies. It has further been known that many species are of coastal plain derivation, and this fact is so anomalous in the Middle West that for some time it has struck the attention of observers.

It is hardly to be supposed that the presence of the coastal plain flora in the neighborhood of the Great Lakes is to be explained on the basis of any accidental or deliberate introduction. Few of the coastal plain plants are of an aggressive or weed-like nature. There is no evidence that plants of conservative habits and habitats, such as *Rynchospora macrostachya*, *Drosera longifolia*, *Polygala cruciata* or *Utricularia gibba* follow the footsteps of man or occur as casual weeds.

Therefore, the presence in the flora of the Lake Michigan region alone of some sixty species of plants which are not found, or are but rarely found elsewhere off the true coastal plain, has long awaited some sort of explanation. With the plan of solving this problem, I went into the field in Indiana and Michigan in the summer of 1920 and collected as many coastal plain and other types of plants as I could. But in work at the Gray Herbarium of Harvard University, it at length became evident that the problem of this anomalous distribution could not be solved without reference to the flora of the Great Lakes as a whole and accordingly a study of the costal plain element of the other lakes was undertaken.

For this purpose I had recourse to the Gray Herbarium and, by the courtesy of Dr. Millspaugh and Dr. Pennell, the herbaria in Chicago and New York were referred to through correspondence. Mr. Charles C. Deam, State Forester of Indiana, kindly assisted me by furnishing notes of his collections in Indiana. And, lastly, reference was had to the writings of many authors citied in the text. The present paper is the summary of these investigations.

Definition of the Coastal Plain Element.

The coastal plain of the geologists is that flat area lying between the coast and the piedmont and extending from the Gulf of Mexico to southern New England. It is usually underlaid by Cretaceous deposits but in various areas and especially on its northward extensions is overlaid with Tertiary sands. But by the coastal plain *flora* is meant the flora of that area of acid bogs, sand barrens, savannahs and marshes anywhere from the Gulf of Mexico and Florida to Cape Cod, Nova Scotia and Newfoundland. It does not include the flora of salt marshes, estuaries, the piedmont country which lies just back of the coastal plain and parallel to it, nor does it include any of those plants which, though abundant on the coastal plain are found in a fairly general way upon other areas, such as *Cenchrus carolinianus, Quercus ilicifolia, Strophostyles helvola, Tephrosia virginiana, Lespedeza capitata,* etc. I have, however, included in the list of inland extensions of the coastal plain some species of the dunes and strands of the Atlantic coast. The dunes and strands, it is true, are better considered as littoral features than as strictly of the coastal plain and its floristic extensions which are characterized rather by savannahs and pondholes and accompanying features than by moving sand and wave-beaten shores. The coastal plain is covered by a very distinctive and endemic vegetation. But the dunes are characterized by plants which occur or have close affinities with species occurring more generally around the basin of the North Atlantic, and extend inland with a greater frequency than the coastal plain species. These in cases where they tend to follow coastal plain ranges, I have included in the coastal plain element. It is thus clear that in speaking of the "coastal plain," I shall have in mind that of the botanist rather than the geologist.

Inland Extensions of the Coastal Plain Flora.

Soil and other controlling conditions of the coastal plain are duplicated in inland stations at various points, and in such places iso-

lated "islands" of the coastal plain flora are likely to be encountered. Such "islands" are to be found along the Great Lakes and on some of the lakes of New York State. They also occur around Havana, Illinois, and at other points on the Illinois River, and there are various small stations on acid bogs of the Middle West. The extensions of the coastal plain flora on the eastern sides of the Appalachians occur chiefly as arms reaching up high, abandoned, sandy flood-plains and are not anomalous, being directly connected with the coastal plain. Or such "islands" may occur as localized colonies in southern New England, Nova Scotia, eastern New Brunswick and Newfoundland—a type of distribution with which we have not to do here.

In the flora of the Lake Michigan area, at least, there are two general types of inland extension from the coastal plain. The first type is the very discontinuous range. In many cases of this kind there are no known stations between the Atlantic coast and the southern end of Lake Michigan. Such a range is that of *Eleocharis melanocarpa,* which is mapped in Figure 1. This is not only typical for the coastal plain but for its "jump" or reappearance on the shores of Lake Michigan. About one third of all the coastal plain species of this area show a roughly similar range with, perhaps, one additional station in New York State or on one of the other Great Lakes.

It is plants of this anomalous range which cause the greatest perplexities to the student of plant distribution and it would indeed be hard to formulate any plausible explanation were it not for the coastal plain extensions of the second type.

Figure 2 shows the range of *Euphorbia polygonifolia.* This little plant of the sea strands also occurs in a general way around the Great Lakes. Such a range is not so difficult to explain as the preceding type and is in itself highly suggestive of an explanation. The majority of the coastal plain species show a similar range. There exist all degrees of continuity between the *Eleocharis melanocarpa* type of range and that of *Euphorbia polygonifolia.* This makes it seem probable that whatever explanation of the second type of range may be offered will be equally well applied to the first type, since the difference is only one of degree.

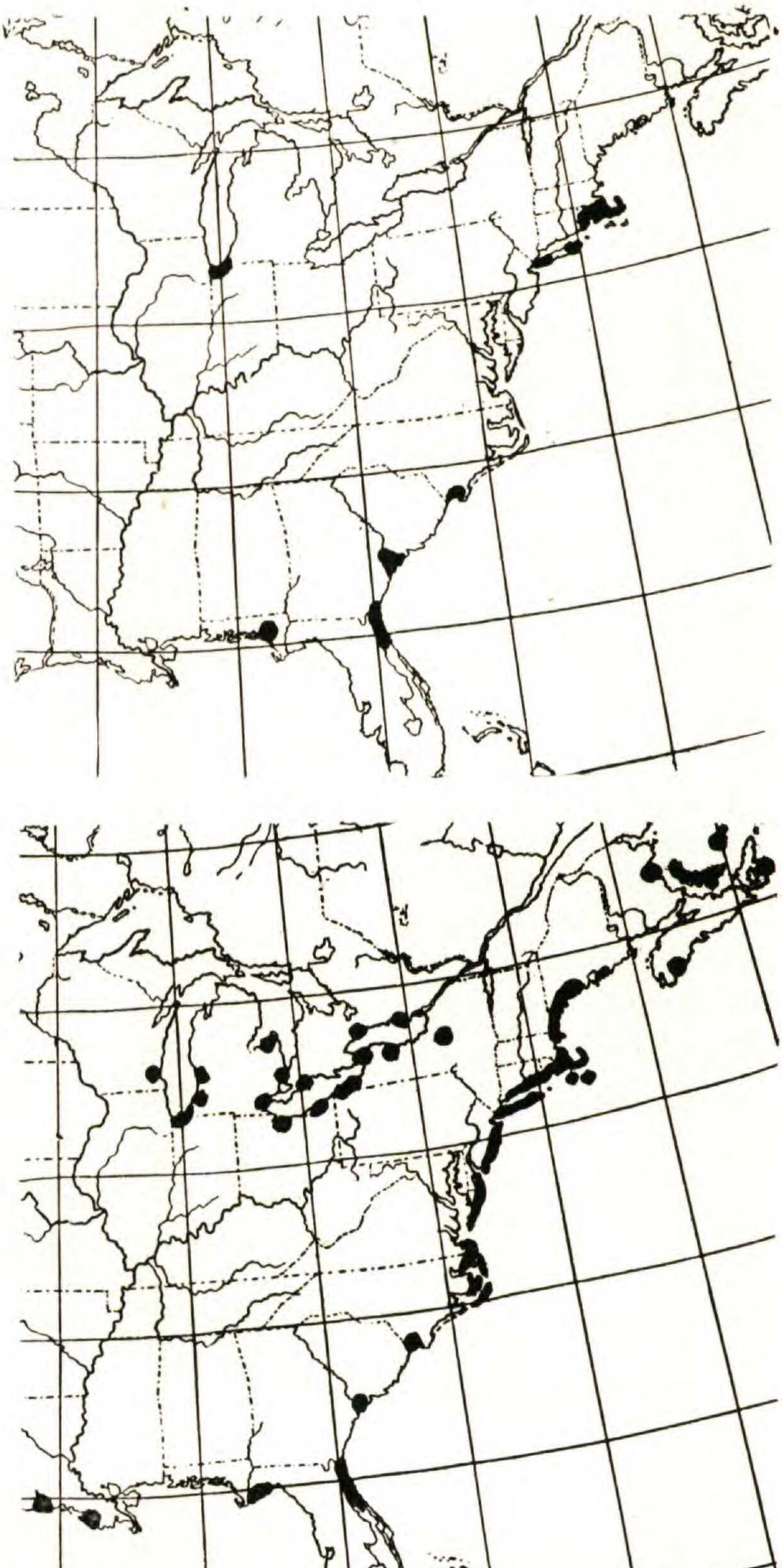

Fig. 1. (above). Range of Eleocharis melanocarpa (area in southern New Jersey inadvertently omitted in copying).
Fig. 2. (below). Range of Euphorbia polygonifolia.

Endemic Species of the Great Lakes.

Many endemic species, wherever they may occur, are closely and obviously related to some other species of characteristic range, so that it is common to speak of a given endemic as "derived" from some other species. And where a variety of a species is endemic there is usually no doubt that the variety is a geographic, as well as an evolutionary, offshoot from the true species.

In the flora of the Great Lakes there are a number of endemic plants and around Lake Michigan, where most are represented, some of them such as *Eleocharis caribaea* var. *dispar* (*E. capitata* var. *dispar*) are undoubtedly of coastal plain origin. In consideration of their clear derivation, it has been thought reasonable to reckon them among the total of the coastal plain element in the flora of the Great Lakes.

Types General in Acid Soil.

There are a certain number of plants which might by some be considered coastal plain species but which are too general in distribution off the coastal plain to belong in that category and yet they are too restricted to be classed as general types of eastern North America. Such a plant is *Eriocaulon septangulare* (*E. articulatum*) which is found locally on acid, sandy or peaty shores and extends inland particularly over the granitic or acid areas of the northern United States and southern Canada. This plant and others like it I have called a type general in acid soil and such plants have not been reckoned into the synopsis of inland extensions of coastal plain species.

Former Extensive Distribution of Coastal Plain Species.

Trying now to account for the presence in the Middle West of the coastal plain flora as we have defined it, we may consider the possible methods of distribution by which it could have spread as it has. It must be remembered that many of the coastal plain types which occur around the head of Lake Michigan make a "jump"—that is, they are lacking or almost entirely lacking from the intervening area. If such species are found one thousand miles apart, without intervening stations, it is obvious that this remarkable distribution is not to be accounted for by that stock method—a most overworked and uncritical method—of dispersal by birds[1], nor yet by winds. Were it by winds, we might expect to find these types as abundantly away from the Great Lakes as near them.

[1] See Fernald, Botanical Expedition to Newfoundland, Rhodora xiii. 143–145 (1911).

Is it not more reasonable to take up what is, in reality, the only remaining hypothesis—namely, that the coastal plain flora was at some time far more extensive around the Great Lakes than it is at present, and that this fact was due to the prevalence, in ancient times, of conditions favorable to its spread? We may conclude that these conditions—which obtain at the present over only very restricted areas—represent conditions at one time fairly general everywhere between the coastal plain and the farthest outlying extensions of its flora.

Summary of the Flora of Some Inland Sand Deposits.

Since the coastal plain flora in its inland extensions seems generally to be associated with sand deposits, it may be well to glance at the localities and vegetation of some dune areas.

Presque Isle is a big "hook" on the Pennsylvania shore of Lake Erie, composed of sand spits, dunes and lagoons. The flora of this area contains 439 species, 18 varieties and one hybrid[1]. About 15 species are coastal plain types, or offshoots from them. Very similar in character are the sands of Indiana, where high dunes, bogs, lagoons and old sand spits abound. Here there are about sixty coastal plain types and related offshoots. Of somewhat different character are the sand deposits of the Illinois River[2]. Here are sandy wastes and dunes where little strand or lagoon life is represented, with the result that the number of coastal plain species falls off to about six.

If now the plant life of the Nebraska dunes be examined[3] we find that there is not a single species[4] which might be classed as commonly restricted to the coastal plain, although a few, such as *Chenopodium leptophyllum* and *Rumex maritimus* var *fueginus* ("*R. persicaroides*") which abound in subsaline regions of the interior, are found on the sea-beaches or brackish sands of eastern America.

[1] According to Jennings, An Ecological Survey of Presque Isle, Erie County, Pennsylvania, Ann. Carneg. Mus. v, 289–421.

[2] See Gleason, Vegetation of the Inland Sand Deposits of Illinois, Bull. Ill. State Lab. Nat. Hist. ix, 23–174.

[3] See Rydberg, Flora of the Sand Hills of Nebraska, Contrib. U. S. Nat. Herb. iii. 133–203.

[4] Rydberg lists *Potamogeton Oakesianus* from Nebraska, but the report seems doubtful.

The Coastal Plain Extensions Connected only with the Great Lakes.

We have seen that the coastal plain types are closely associated with the Great Lakes and that away from these waters and from the lakes or rivers connected with them, there are no stations where any considerable number of coastal plain plants occur. They form, in various areas along the Great Lakes, as they do not elsewhere off the true coastal strip, a conspicuous part of the vegetation. Of course, the Mississippi Valley is an exception. It abounds in coastal plain types but it is not a discontinuous sort of extension but rather forms an arm of the flora of the basin of the Gulf of Mexico, and as such it is noticeable that not many of the coastal plain types which characterize the Mississippi Valley are the same as those which are found extended along the Great Lakes. The Mohawk Valley and the Finger Lakes of New York State might also be taken as exceptions, in that they are not outlets or tributaries of the Great Lakes. But it will be possible to show that in times not far distant they were precisely these.

Glacial History of the Great Lakes.

The Wisconsin Ice Sheet destroyed all plant life in the glaciated area, so that all the vegetation around the Great Lakes can have come there only in post-pleistocene times. The interest for the botanist begins during the important period when the glacier was receding for the last time and the Great Lakes were in process of formation. This period has been thoroughly investigated and described by Leverett and Taylor in *The Pleistocene in Indiana and Michigan and the History of the Great Lakes*[1]. This we may summarize as follows:

The glacier had piled up and left in the course of its various advances and recessions a border of moraines fringing the lakes which lay to the south. The moraines exist more or less along the whole vast extent of the margin, but nowhere are they more marked than over the rolling country of Ohio, Michigan, Indiana, Illinois, and Wisconsin. As the ice receded the great melting floods poured out from its edge, and, meeting with the moraines, were dammed back into the pre-glacial river systems to the north which had been deepened by glacial gouging.

[1] Monographs of the U. S. Geol. Surv. iii.

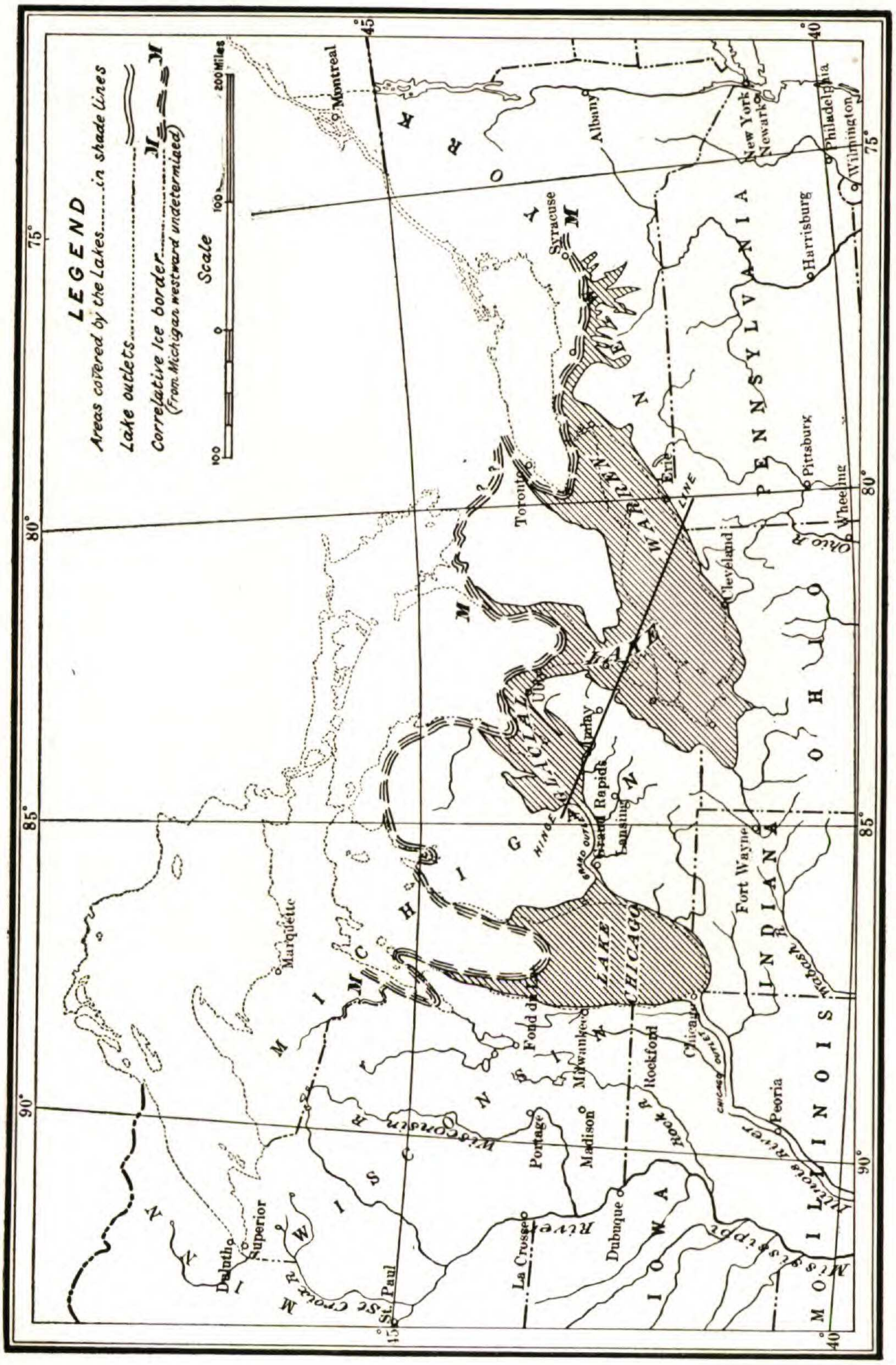

Fig. 3. Lakes Chicago and Warren Stage.

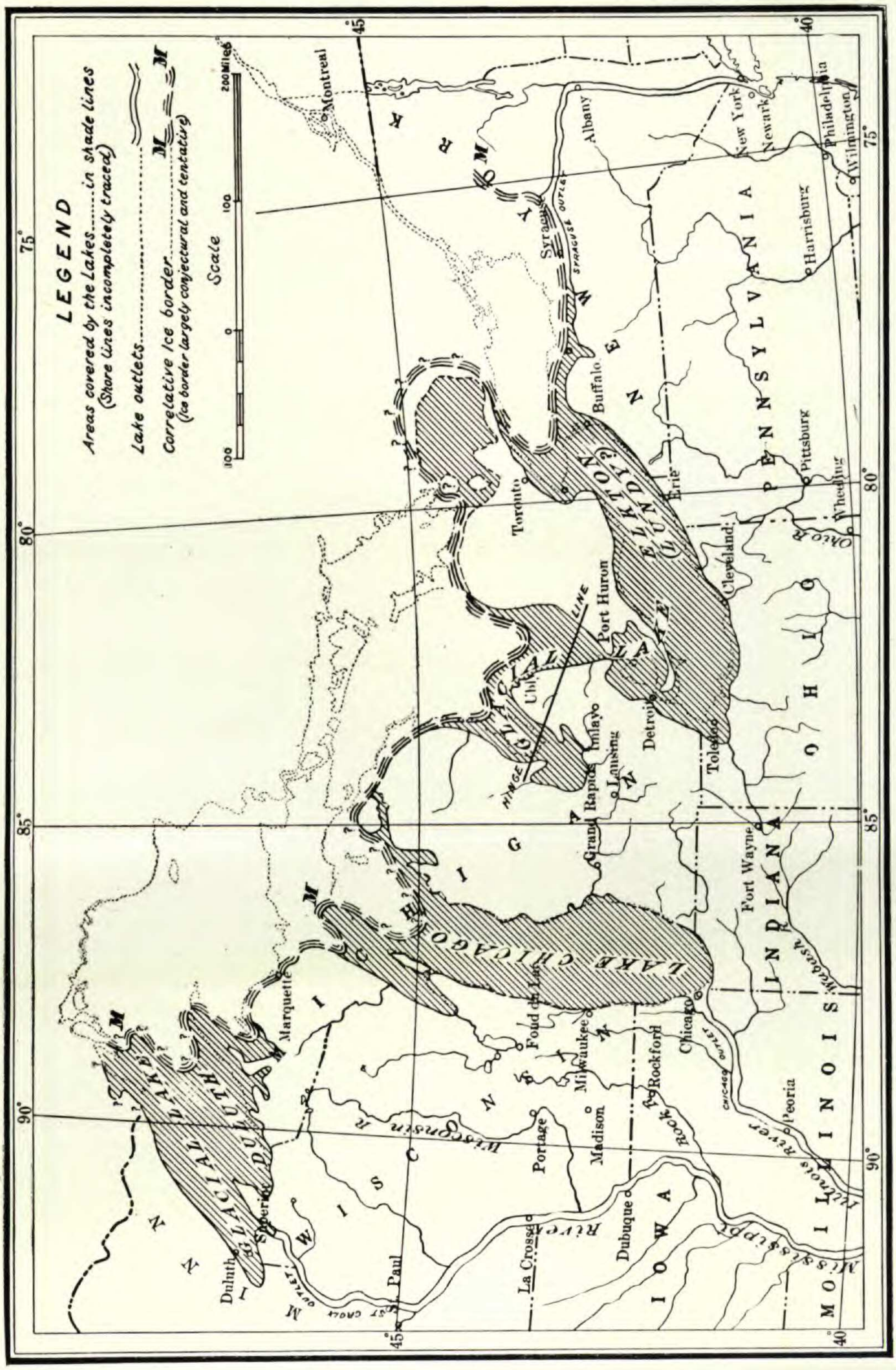

Fig. 4. Lakes Chicago and Elkton of Lundy Stage.

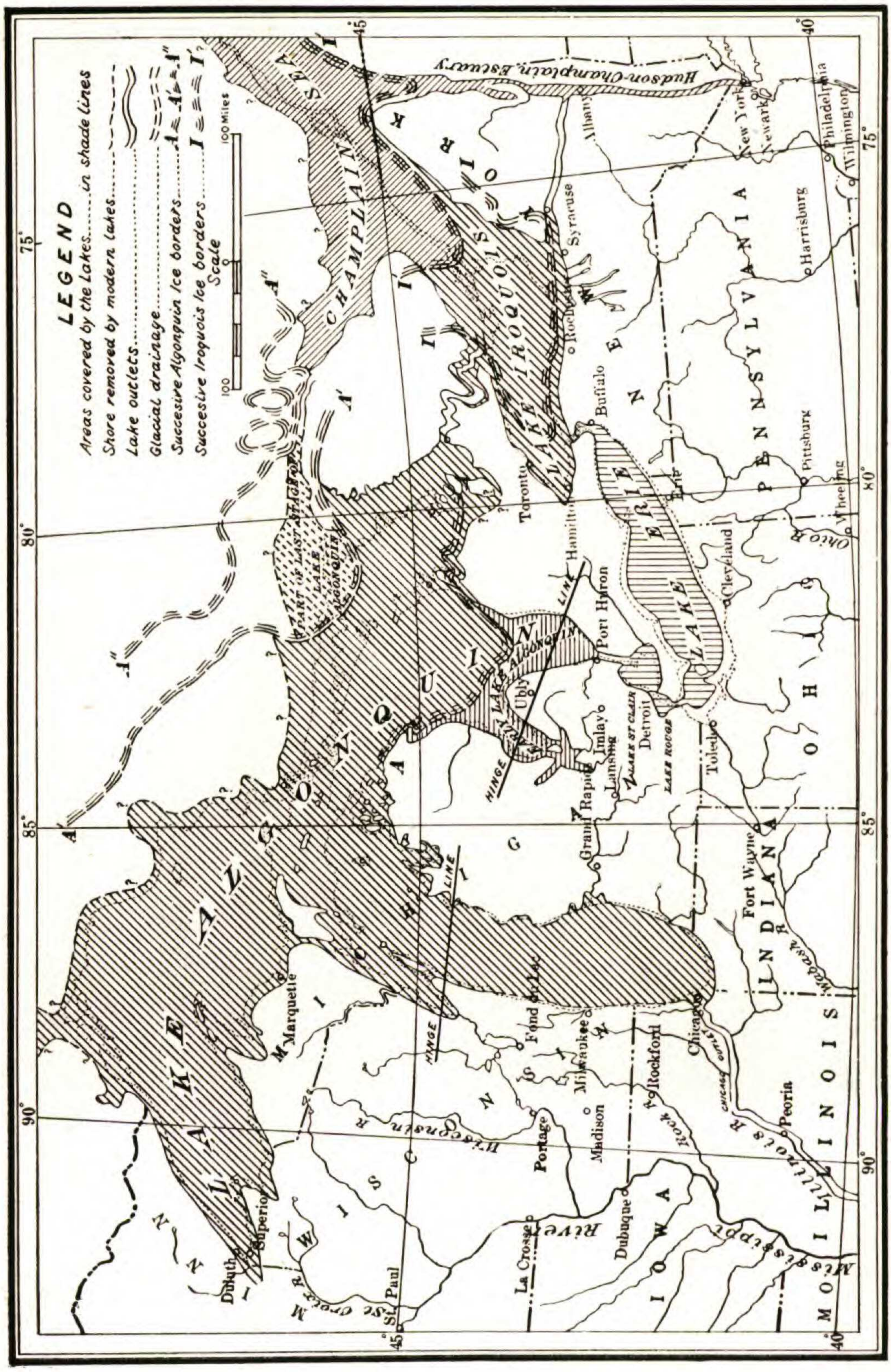

Fig. 5. Lake Algonquin Stage.

In this manner the Great Lakes began to form, and they rose until a low point was found in the barriers to the south or until the receding ice uncovered outlets to the north. First one outlet and then another functioned, as the alternate advances and retreats of the ice altered the height of the water, and as the land tipped with the release of static pressure exerted by the glacier. As a consequence the lakes many times changed their level, shape, and direction of outflow, but for us only the last stages are important. Whatever vegetation may have followed the first retreats of the glacier, it must have been wiped out again at each readvance. But when the ice had receded for the last time, it left in undisturbed possession of the soil some sort of vegetation of which we may expect to find traces to the present day.

Figure 3 is a map of glacial Lakes Chicago and Warren and the connectives, consisting of the Grand River across Michigan and the Finger Lakes and Mohawk-Hudson system of connection with the ocean. The continuous character of what are now Lakes Michigan and Erie is plainly shown and some suggestion of their connection eastward is indicated.

In Figure 4 we have another and subsequent stage in the history of the Great Lakes. This is the Lakes Duluth, Chicago, and Lundy stage. The Grand River connective is considered as probably not functioning at this time, but an exceedingly large Mohawk-Hudson connective with the ocean is affirmed[1]. In Figure 5[2] we have the Algonquin stage. The Great Lakes are now at a maximum, all joined by wide connectives and opening very distinctly into the Champlain Sea. The Mohawk-Hudson connective is functioning, and the ice has retreated well away from the lakes.

Migration of the Coastal Plain Flora.

The glacier never returned after this. The evidence indicates that during the Algonquin stage there undoubtedly took place a shore-wise migration of the coastal plain flora. It might be well questioned whether the migration did not take place in one of the periods preceding. It is hard to fix the exact time and this might appear dogmatic, but during the last of the Algonquin stage, at least, there was certainly ample opportunity for such a migration, and there is evidence that it did then occur.

[1] I am aware that some geologists challenge the existence of this connective, but the evidence of the plants is conclusively for it, as I shall show.

[2] Figs. 3, 4, 5, are reproduced from Taylor, The Glacial and Post Glacial History of the Great Lakes Region, Rep. Smiths. Inst. 1912, 291–327, by the kind permission of Mr. Taylor and of the Smithsonian Institution.

As for the possibility of migration before that time, there is some evidence that migration also took place in the Lakes Chicago and Warren stage, shown in Figure 3. The reason for thus thinking is that so many coastal plain species are found in the present valley of the Grand River in Michigan which, during the stage just referred to (but not later) formed the only connective between Lake Chicago and Lake Warren. According to Leverett and Taylor, this connective ceased to function after this stage. Hence any plants which now persist along the Grand River Valley probably owe their presence to migration during the period earlier than the Algonquin stage, when the Grand River connective was functioning.

On the other hand, it is not perfectly certain that this outlet did not function at later periods of time, and it must be admitted that, with the glacier very close at hand, the period of the Grand River connection was certainly the earliest possible opportunity for the migration and is, perhaps, too early to conform with most of the facts as we know them.

Certainly the migration did not occur much *later* than the Algonquin stage, that is, it is not now going on. This we know because the number of stations for localized coastal plain species has not materially increased during the period of observation on the region. And we know it from the fact that the conditions which favored the spread of coastal plain plants—conditions of which we shall speak later—soon ceased to exist in any general way after the close of the Algonquin.

Place of Coastal Plain Plants in Erosion Cycles and Plant Succession.

It is a remarkable fact that there are many more coastal plain species on Lake Michigan, nearly one thousand miles from the Atlantic, than on Lake Erie, four hundred miles nearer. This I believe to be due to the chance that conditions around the head of Lake Michigan are more favorable to the preservation of plants with habits like those of the coastal plain. There are rarely found on Lake Erie such superlative conditions as exist on Lake Michigan at Pine or Dune Park, Indiana. Indeed, the conditions on the Great Lakes as a whole have now become fairly stabilized. The supply of water is probably in an approximate equilibrium with the loss, so that no changes of level, save seasonal ones, are taking place and the currents have silted up the bays, while the storms have worn away the weaker

promontories. This stability is so favorable to the advance of a vegetation more vascular than that which ordinarily characterizes the coastal plain, that thickets and forests are slowly taking possession on those shores and the coastal plain types are being crowded out.

It is noticeable that those species which show the greatest discontinuity of range, as exemplified by *Eleocharis melanocarpa*, are in most cases inhabitants of the more transitory of the littoral physiographic features—the ponds, pond-margins, and lagoons; while it is those plants of the second type, plants of dunes and strands such as *Euphorbia polygonifolia*, which have tended to persist along the Great Lakes. The discontinuity of the first type would point to a dying-out, and the persistence of the type of dunes and strands merely means that while there are any Great Lakes, there must always be a strand, and also there will usually be dunes.

In general, the coastal plain types persist only where those younger and less-permanent features of the shore erosion cycle are still to be found, and they themselves represent the younger stages of plant succession. Such is the case at Presque Isle, where the whole island has been shown by direct observations over the course of a century to be moving eastward, the west shores being washed away by a prevailing current, and the east being built out by spits. And the Indiana shores of Lake Michigan represent a long series in the cycles of shore erosion and more particularly of lake recession. One may observe there all stages from new barrier beaches and lagoons to shores which have been dry of water for thousands of years.

The coastal plain element follows closely the shores of the lakes as they recede, and the field and forest types of the adjacent country press hard upon it; indeed the coastal plain plants prepare the ground for their successors. By the larger measures of time, the coastal plain element in this region is rather ephemeral, though if the balance of nature is not disturbed by man, it will probably never be entirely eliminated. This pioneering quality of the coastal plain type is, really a further proof of the early migration around the glacial lakes. These plants probably then were, for the same reasons that they now are, biologically well adapted to pressing forward quickly on the unstable margins of these lakes, while the forest types would naturally return more slowly.

Climate at the Close of the Glacial Period.

It may well be questioned whether or not the conditions of life which obtained at the close of the glacial period were suitable for the migragration of coastal plain plants. This question cannot be answered very specifically, for no one knows exactly what were the conditions of life at this time. But I shall give such evidence as there is.

As to climate: it might at first thought appear that it would have been too cold for coastal plain plants. But it has amply been shown upon the best authorities that coastal plain plants have a tendency to range up and down the coastal plain from Florida to Nova Scotia and Newfoundland without very great regard to the variabilities of the several climates of this territory, but with regard chiefly to the acid character of the sands and peats which there abound. It is probable, therefore, that even were the climate of the Algonquin stage fairly rigorous, there might still be an abundance of such types growing along the glacial lakes.

But it is, perhaps, not necessary, to imagine a polar frigidity for this stage. The amount of insolation required to melt back the glacier must have been very great and as the earth and its vegetation have a high coefficient of heat absorption, they received at that time a significant amount of warmth[1].

That it was warm enough for plant life between the glacial advances is proven by the fact of peat deposits found *between* glacial deposits[2]. This furnishes proof that whatever the climate and the length of the interglacial periods, there were not only abundant time but appropriate conditions for a plant growth sufficient to make considerable peat deposits.

But the glacier might reasonably be expected to make the waters of its marginal lakes cold. Even if this were so, it is still true that the coastwise lagoons and bays would be shallow and protected, and hence would soon heat up. It is in these, or on their margins, assuredly, and not in the open waters of the big lakes, that the coastal plain flora must have migrated. Terrestrial types would not have been much affected by the temperatures of the adjacent waters.

[1] The whole matter of climate at this time has been treated by Dachnowski, Peat Deposits and Their Evidence of Climatic Change, Bot. Gaz. lxxii., summarized on pages 85–86 (1921).

[2] Chicago Folio of the U. S. Geol. Surv. 11.

(*To be continued.*)